Study on Biological Characteristics of Ammonia-oxidizing Archaea in the Ocean

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Chapter 1 General introduction

1.1 Oceanic archaea

1.1.1 Taxonomy

Since the concept of Archaea has been presented by Woose and Fox in 1977 (Woose and Fox, 1977), Archaea had been defined into two phylums, *Euryarchaeota* and *Crenarchaeota* (Woose *et al.*, 1990), and been considered as a kind of microorganism habiting in particular extreme environment. Among these two phylums, *Euryarchaeota* includes methanogenic archaea, highly halophilic archaea, thermophilic and acidophilic archaea as well as some hyperthermophilic archaea, while Crenarchaeota includes hyperthermophilic archaea. (Fig. 1-1)

Reported by DeLong in 1992, archaea was first proved to exist in a wide variety of environment, not only in some particular extreme environment (DeLong, 1992; Fuhrman *et al.*, 1992). Different from extremophilic archaea, marine mesophilic archaea can be devided into four phylogenetic groups: Marine Group Ⅰ~Ⅳ. Among these four groups, Marine Goup Ⅰ is a phylogenetic group belonging to *Crenarchaeota* (DeLong, 1992). And the other three groups (Marine Group Ⅱ~Ⅳ) are belonging to *Euryarchaeota* (Delong, 1992; Fuhrman and Davis, 1997; López-Garcia *et al.*, 2001). However, only few isolates in these groups are available yet, and their biological role in the environment remains to be fully elucidated.

Marine Group Ⅰ is actually a distinct phylogenetic group which is phylogenetically close to the group of hyperthermophilic *Crenarchaeota* (DeLong, 1992). Recently, the concept of the third phylum of archaea: Thaumarchaeota (which comprises the phylogenetic group of Marine Group Ⅰ) has been proposed (Brochier-Armanet *et al*., 2008), and being supported by many researchers (Brochier-Armanet *et al*., 2012; Pester *et al.,* 2011; Spang *et al.,* 2010; Walker *et al.,* 2010). Organisms in this phylum are generally mesophilic, and globally distributed and are found in high numbers in marine and freshwater environments, soils, and sediments.

Marine Group Ⅰ and Marine Group Ⅱ are the most abundant groups existing in the global ocean among marine archaea (DeLong *et al.,* 1999; Karner *et al.*, 2001). And Marine Group I is one of the main members of planktonic prokaryotes, accounting for 40~50% of

bathypelagic prokaryotes, and 20% of total oceanic prokaryotes (Karner *et al.*, 2001). Marine Group Ⅱ are dominant in euphotic zone in temperate oceans, and existing in a variety of environment including the Antarctic Ocean (Massana *et al.*, 1998, 2000; Murrey *et al.*, 1999).

1.1.2 Involvement of archaea in biogeochemical cycle

The biogeochemistry of our planet is shaped by the microbes-driven biological fluxes of the elements, particularly the six major building blocks of life: hydrogen, carbon, nitrogen, sulfur, oxygen and phosphorus. Since the concept 'biogeochemistry' has been proposed from 1926, only bacteria and eukarya were considered contribute to these nutrients cycles. The domain archaea, which had been thought to be habit only in extreme environemtns, were first described in the biogeochemical cycle until 50 years later (Woese and Fox, 1977). The role and significance of archaea started to be realized since early 1990, until the ubiquity and diversity of oceanic planktonic archaea has been recognized (DeLong et al., 1992; Fuhrman et al., 1992). Using molecular biological, biochemical and isotope-based methods, evidences began to accumulate proving that archaea are important contributors in carbon and nitrogen cycling.

Archaea in the nitrogen cycle

In the nitrogen cycle, archaea get involved in the fixation of dinitrogen gas, as the methanogenic archaea has the ability to fix dinitrogen gas; archaea also participate in denitrification process, as a few cultivated archaea are capable of denitrification. However, the most important role of archaea in the nitrogen cycle is they can aerobically oxidize ammonia into nitrite, and thus recently archaea has been recognized as the main driver of nitrification in various ecosystems (i.e. reviewed by Offre et al., 2013).

Archaea in the carbon cycle

Many cultivated representatives of Crenarchaeota, Thaumarchaeota and Euryarchaeota are capable of autotrophic growth, as they assimilate carbon from oxidized inorganic compounds such as carbon dioxide or bicarbonate (Berg et al., 2010). Nevertheless, many autotrophic members of the Archaea can grow mixotrophically, as they can coassimilate small organic compounds under suitable conditions or switch between an autotrophic and a heterotrophic

lifestyle (Kletzin, 2007).

Methane, a major greenhouse gas but also an important source of energy for humans, is the predominant hydrocarbon in earth's atmosphere. Methanogenic archaea, affiliated with Euryarchaeota, are strict anaerobes that produce methane as the major product of their energy conserving metabolism. Archaea dominate the biogenic production of methane, but also key to the oxidation of this important hydrocarbon. Some close relatives of methanogenic archaea play a critical role in controlling the emissions of methane, by oxidizing methane back to CO_2. The methane-oxidizing archaea are also strict anaerobes and affiliated to Euryarchaeota. (i.e. reviewed by Offre et al., 2013)

1.2 Global nitrogen cycle

1.2.1 Marine nitrogen cycle

Nitrogen is biologically limiting element and an essensial nutrient element to all living organisms in the planet. Although ca. 79% of the air is consist of nitrogen gas (N_2), this stable form of nitrogen cannot be utilized by most living organisms because the triple bound structure is difficult and energetically cost to break. Thus, the fixed form of nitrogen, referring to any reactive form of nitrogen (such as nitrate, nitrite and ammonia…), are required by most living organisms (such as algae, and microbes…). The processes governing transitions from one form of nitrogen to another are all part of the nitrogen cycle. (Fig. 1-2)

At global scale, biological nitrogen fixation if the largest source of nitrogen to the ocean, while the anaerobic microbial processes are the main export of nitrogen losses (Francis et al., 2005; Galloway, et al., 2004; Gruber et al., 1997). Nevertheless, the biological nitrogen fixation and anaerobic nitrogen losses are ultimately connected by nitrification, the microbe-driven oxidation from ammonium to nitrite and nitrate. Every year, ca. 4×10^{11} kg of nitrogen cycles through the ocean each year (Francis et al., 2005; Galloway, et al., 2004), and nearly all of this nitrogen has to be nitrified at least once (Karl, 2002). Given that nitrification controls the global nitrogen balance, this process is one of the most important ocean processes in global marine nitrification.

1.2.2 Ammonia oxidation

Ammonia oxidation is the first step and rate-limiting step of nitrification, the microbially mediated pathway for the conversion of ammonia to nitrite. It has long been considered that ammonia oxidation is conducted only by microorganisms from the domain *Bacteria*: the betaproteobacteria (β- Ammonia-oxidizing Bacteria; β-AOB) from the genus *Nitrosomonas* and *Nitrosospira* (Purkhold et al., 2000; 2003; Beaumont et al., 2004; Taylor and Bottomley, 2006) and the gammaproteobacteria (γ- Ammonia-oxidizing Bacteria; γ-AOB) from the genus *Nitrosococcus* (Ward and O'Mullan, 2002). However, these two groups of AOB often comprise only 0.1% of the bacterial assemblages (Ward et al., 2000). Until 2004, based on the discovery of a unique ammonia monooxygenase gene (*amoA* gene) on archaea domain (Vent et al., 2004), the involvement of archaea in nitrification was first suggested. Since then, the ubiquity and diversity of ammonia-oxidizing archaea (AOA) has been increasingly recognized, and these ammonia-oxidizing archaea were found specifically associated with the pelagic non-thermophilic marine thaumarchaeota (Beman et al., 2006; Agogue et al., 2008; Cafferey et al., 2007; Coolen et al., 2007; Lam et al., 2007; Santoro et al., 2008). In contrast to the low abundance of AOB reported in various eco-systems, thaumarchaeota are ubiquitous and abundant in the ocean (DeLong et al., 1994; Stein and Simon, 1996; Karner et al., 2001; Herndl et al., 2005; Ingalls et al., 2006), and often account for ca. 20% of all prokaryotic cells in the global ocean (Karner et al., 2001). Thus, the archaea-driven nitrification may play an important role in global oceanic nitrogen cycle, whereas the potential relative contribution of bacterial nitrification and archaeal nitrification in natural waters still remain to be fully elucidated.

1.3 Some open questions about ammonia-oxidizing archaea

1.3.1 Relative distribution of ammonia-oxidizing archaea and ammonia-oxidizing bacteria

The wide distribution of ammonia-oxidizing archaea (AOA), affiliated with Thaumarchaeota, across a variety of aquatic environments is now well established through reports based on abundance of the gene-encoding archaeal ammoniamonooxygenase α-subunit (*amoA*) in

oceanic waters (Beman et al., 2006; Agogue et al., 2008; Cafferey et al., 2007; Coolen et al., 2007; Lam et al., 2007; Santoro et al., 2008). Nevertheless, the relative contribution of AOA versus AOB remains unclear and factors that regulate ammonia oxidizers' activity and diversity in aquatic ecosystems have not yet been fully elucidated. Geochemical-based approaches and molecular-based approaches targeting both cultured strains and uncultured environmental samples indicate that AOA are very different from AOB, their ammonia-oxidizing bacterial counterparts. Physiological differences between AOA and AOB have been pointed to aspects such as ammonia affinity (Martens-Habbena et al., 2009), substrate range (Könneke et al., 2005; Hallam et al., 2006; Ouverney et al., 2000), and metabolic pathway (Hallam et al., 2006b; Berg et al., 2011; Blainey et al., 2011; Park et al., 2010; Arp et al., 2007). These physiological differences are expected to be vital factors and be reflected in their niche segregation and the observed dynamics of their relative distributions.

1.3.2 Environmental factors affecting the distribution of ammonia-oxidizing archaea

Pelagic marine Thaumarchaeota are typically most abundant below ~100 m depth in the water column (DeLong, 1992; Fuhrman et al., 1992; Massana et al., 1997; Karner et al., 2001; Mincer et al., 2007; Church et al., 2010; Santoro et al., 2010). Previous studies have pointed to environemental factors such as salinity, light, temperature, ammonium, oxygen, and sulfide as major determinants of the distribution of ammonia oxidizing archaea (e.g., Murray et al., 1999; Caffrey et al., 2007; Santoro et al., 2008; Bernhard et al., 2010; Gubry-Rangin et al., 2010), however, the results are often contradictory. For most previous studies, the distributions of AOA have been investigated on the euphotic and mesopelagic zone, where ammonia concentrations are much higher than in waters below 1000 m depth. Thus, a thorough study targeting throughout water column on a large-scale sampling are of great importance for better understand the major environmental regulators of the distribution of AOA.

1.3.3 Thaumarchaeota: autotrophic, heterotrophic or mixotrophic?

The natural radiocarbon content archaeal lipids indicated that thaumarchaeota in ocean

waters predominately grow autotrophically (Ingalls et al., 2006; Pearson et al., 2001; Wutcher et al., 2003). Modeled estimates of archaeal biomass productionin deep waters range from 0.7 to 0.8 Gt C/year, suggesting thaumarchaeota might contribute ca. 1%j of the annual primary production in the ocean (Herndl et al., 2005; Ingalls et al., 2006). However, a potential for mixotrophic growth has been reported from analyses of the genome of *Nitrosopumilus. maritimus* SCM1 and *Ca. Cenarchaeum symbiosum* (Hallam et al., 2006a; 2006b; Walker et al., 2010). And a recent research revealed that two new marine AOA isolates *Nitrosopumilus. maritimus* PS0 and HAC1 were obligate mixotrophs that rely on uptake and assimilation of organic carbon compounds (Qin et al., 2014).

Additionally, a urea-utilization mechanism hypothesized to explain thaumarchaeal nitrification, which has been recently suggested by urea uptake experiments using seawater samples (Alonso-S áez et al., 2012) and isolated marine AOA strains (Qin et al.,2014), shows the presumed significance of an urelytic mechanism under low-energy conditions. However, other studies have shown that transcripts of the functional gene in the urea-utilization mechanism, the *ureC* gene, are not common in surface waters of the Canadian Arctic (Pedneault, et al., 2014) and Marennes-Oléron estuary (Hugoni et al., 2015). Therefore, we still lack sufficient evidence to show the possibility and significance of this urelytic mechanism.

1.4 Oceanography

1.4.1 The Pacific sector of the Arctic Ocean

The Arctic Ocean (Fig. 1-3), located in the northernmost part of the world, is one of the coldest areas in the world. However, the Arctic systems can be rich and diverse habitats for marine life in spite of the extreme cold environment (Grebmeier et al. 2006, 2010). Biological cycling processes and biological communities are directly influenced by changing sea ice extent, light availability, seawater hydrography (such as nutrients, salinity, temperature, density), currents, and water column production (Grebmeier and Maslowski et al., 2014). The retreating sea ice and warming temperature have dramatic impacts on the biological system, such as changes in overlying primary production, altering organic carbon trandformation,

pelagic-benthic production and community structure that could have further effects to higher trophic levels (Grebmeier and Maslowski et al., 2014).

The Pacific sector of the Arctic Ocean is experiencing the greatest seasonal retreat and thinning of sea ice in the Arctic (Grebmeier and Maslowski et al., 2014). In the Pacific sector of the Arctic Ocean, Pacific water transiting across the wide Bering, Chukchi and the eastern portion of the Beaufort Sea, is a major driving force for the physical environmental state, ice extent and thickness, productivity and carbon transport in the Amerasian Arctic (Grebmeier and Maslowski et al., 2014). In this region, the Bering Strait is a major 'gate' and a pathway for fluxes of biological organisms and organic carbon (Grebmeier et al. 2006; Grebmeier, 2012 ; Walsh et al., 2004). Recent estimates on the Bering Strait indicated that freshwater in Bering Strait may procide ca. 40% of the total freshwater input to the Arctic Ocean (Woodgate and Aagaard, 2005). The nutrient rich Pacific waters transit through the Bering Strait, and influence the thermohaline circulation in the Arctic Ocean. Winter and summer Pacific Water types play different roles in the transport of heat, fresh water, nutrients, carbon and biological organisms through the Bering Strait. The warm Pacific summer water is a source of heat and particularly impact the Chukchi Sea area; while the cold Pacific winter water influence the halocline formation (Shimada et al., 2006).

1.4.2 The North Pacific Ocean

The Pacific Ocean (Fig. 1-4) is the largest oceanic division on earth, which connects the Arctic Ocean in the north and the Antarctic Ocean in the south. The Pacific Ocean also extends from Asia and Australia in the west and the Americas in the east, covering 165.25 million square kilometers in area and representing ca. 50% of the global earth's oceanic water (http://global.britannica.com/place/Pacific-Ocean), and thus has an important role in controlling the global climate. The equator divides the Pacific Ocean into North Pacific Ocean and South Pacific Ocean. The motion of Pacific waters is generally clockwise in the North Pacific Gyre and counter-clockwise in the South Pacific Gyre. The North Equatorial Current, driven westward along latitude 15°N by the trade winds, turns north near the Philippines to

become the warm Kuroshio Current.

In the North Pacific Ocean, most of it is covered by the North Pacific Gyre, which locates between the equator and 50°N latitude. The northern part of North Pacific Gyre is the North Pacific Current, which is a slow warm water current that flows west to east between 40°N and 50°N. When it flows near Americas, this current splits into the southward California Current and northward Alaska Current. The southward California Current then moves to the west, joining the North Equatorial Current and circling in the North Pacific Gyre, while the northward Alaska Current then joining a smaller gyre in North Pacific Ocean, the Subpolar Gyre. The counterclockwise Subpolar Gyre forms at high latitudes and circulate along the Siberian Pacific coast and the subpolar areas in the North Pacific Ocean.

1.4.3 The Suruga Bay, Japan

The Suruga Bay (Fig. 1-5) located on the Pacific coast of Honshu in Shizuoka Prefecture, Japan. As the nearby Mount Fuji (Japan's loftiest peak, 3776 m) rises from the 2500 m depth Suruga Trough running up the middle of the bay, Suruga Bay is the deepest nearshore bay in Japan. The Suruga Bay receives numerous fresh water inflows from rivers such as the Oi River, Fuji River, and Abe river from the western side; and the Kano River from the eastern side of Suruga Bay (http://www.isewan-db.go.jp/index.asp). Although the Suruga Bay is open to the Pacific Ocean to the south, it is protected from oceanic waves by Izu Peninsula. Thus, Suruga Bay has been one of the most important deep-sea fishery spot in Japan, famous for its rich fishery species diversity. For reasons above, the Suruga Bay is considered as a perfect research spot for studies on deep-sea organisms in temperate zone.

1.5 Objectives of this study

In order to describe the distribution characteristics of ammonia oxidizing archaea, associated with dynamics of community structure and environmental variables, the abundance, diversity and activity of AOA were compared in three different ocean areas: the Pacific sector of the Arctic Ocean, the North Pacific Ocean, as well as the Suruga Bay in Japan. A total of 173

samples throughout water columns across these three oceans were analyzed based on molecular technologies targeting functional genes and 16S rRNA genes. This study presents a comprehensive description on the distribution characteristics of AOA, which is fundamental to a better understanding on the physiology of AOA, and provide valuable basis for perspectives of global microbial nitrification.

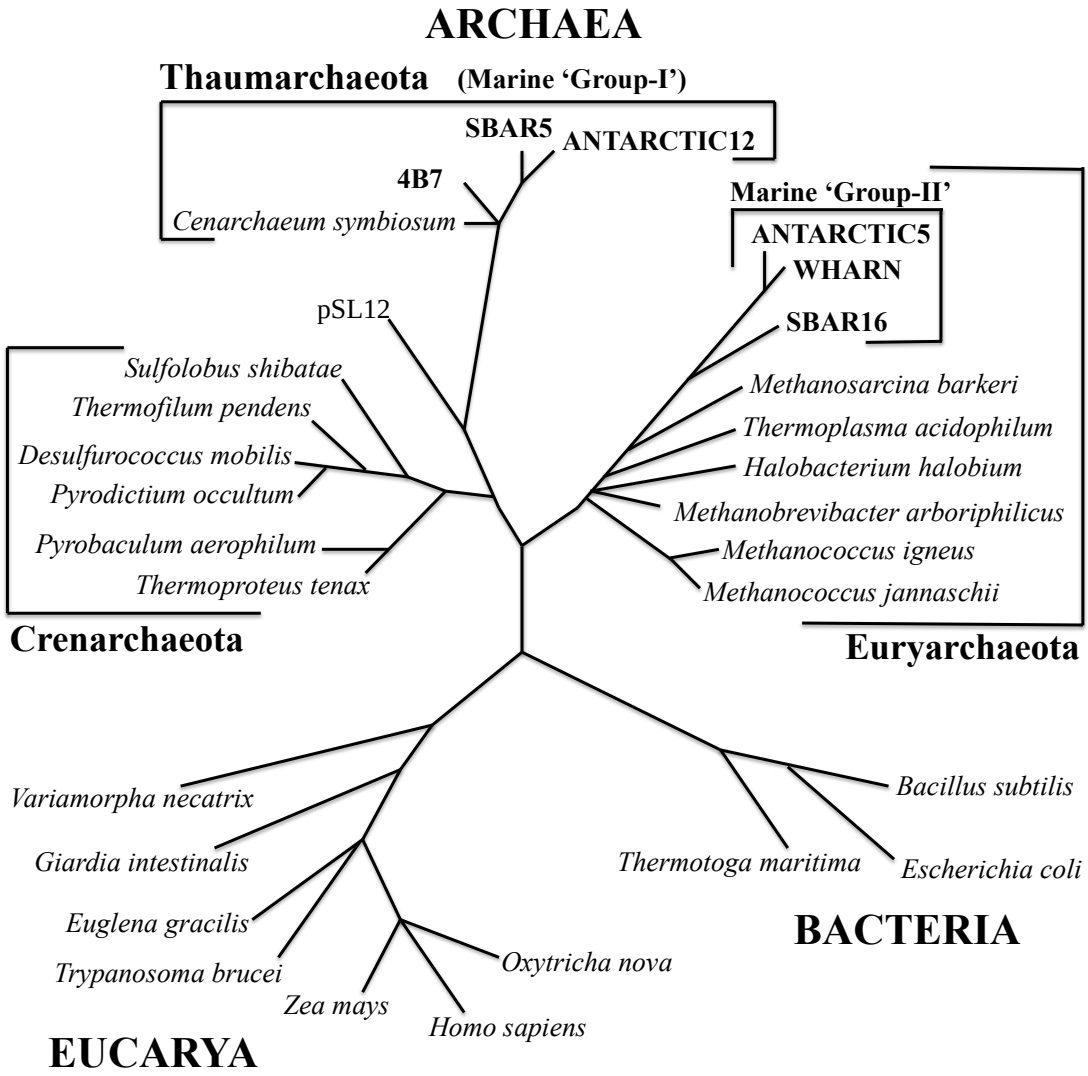

Fig.1-1 Evolutionary relationships of Archaea, Bacteria, and Eucarya. (modified from DeLong et al., 1998)

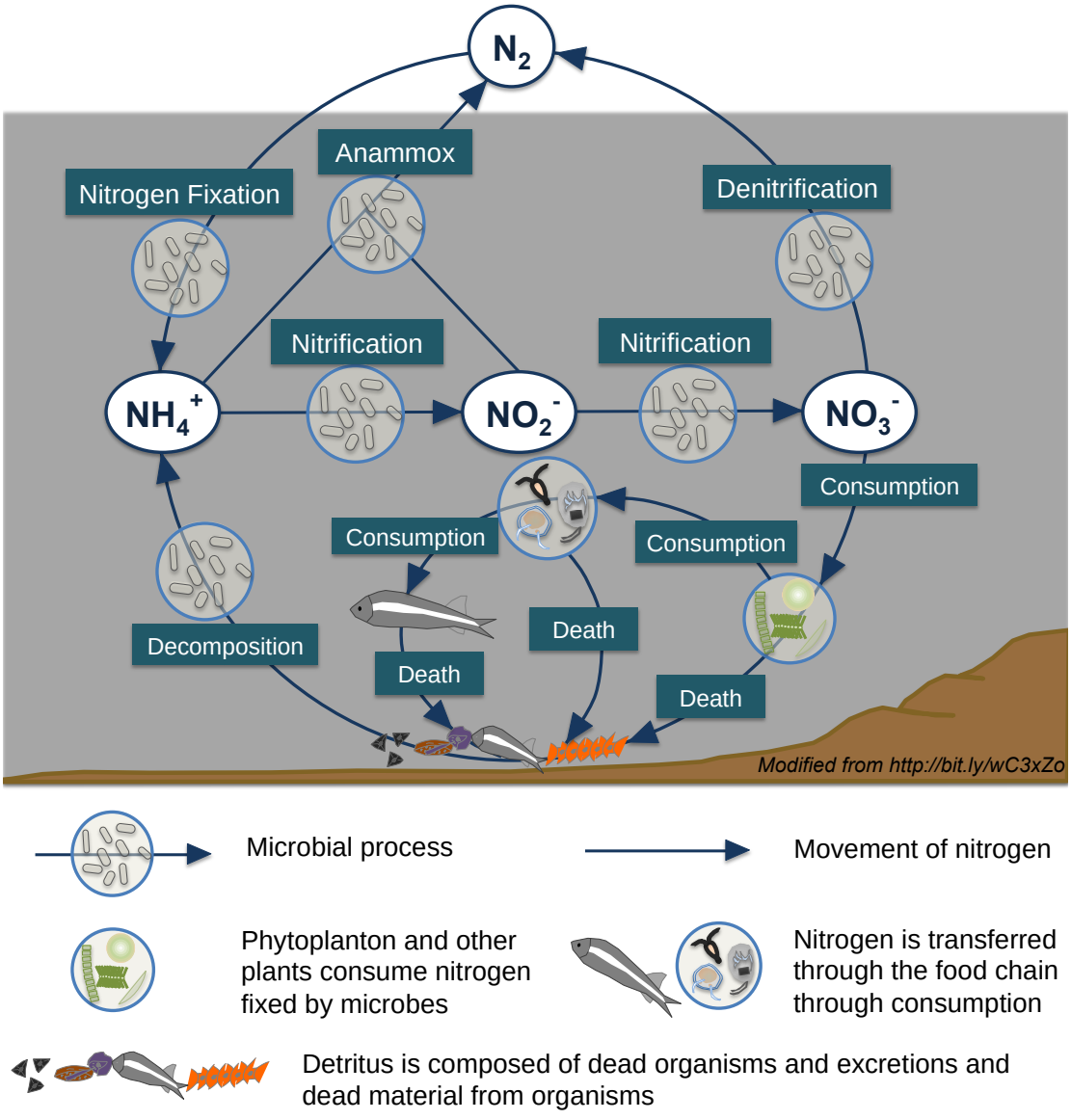

Fig.1-2 Marine nitrogen cycle (modified from *http://bit.ly/wC3xZo*)

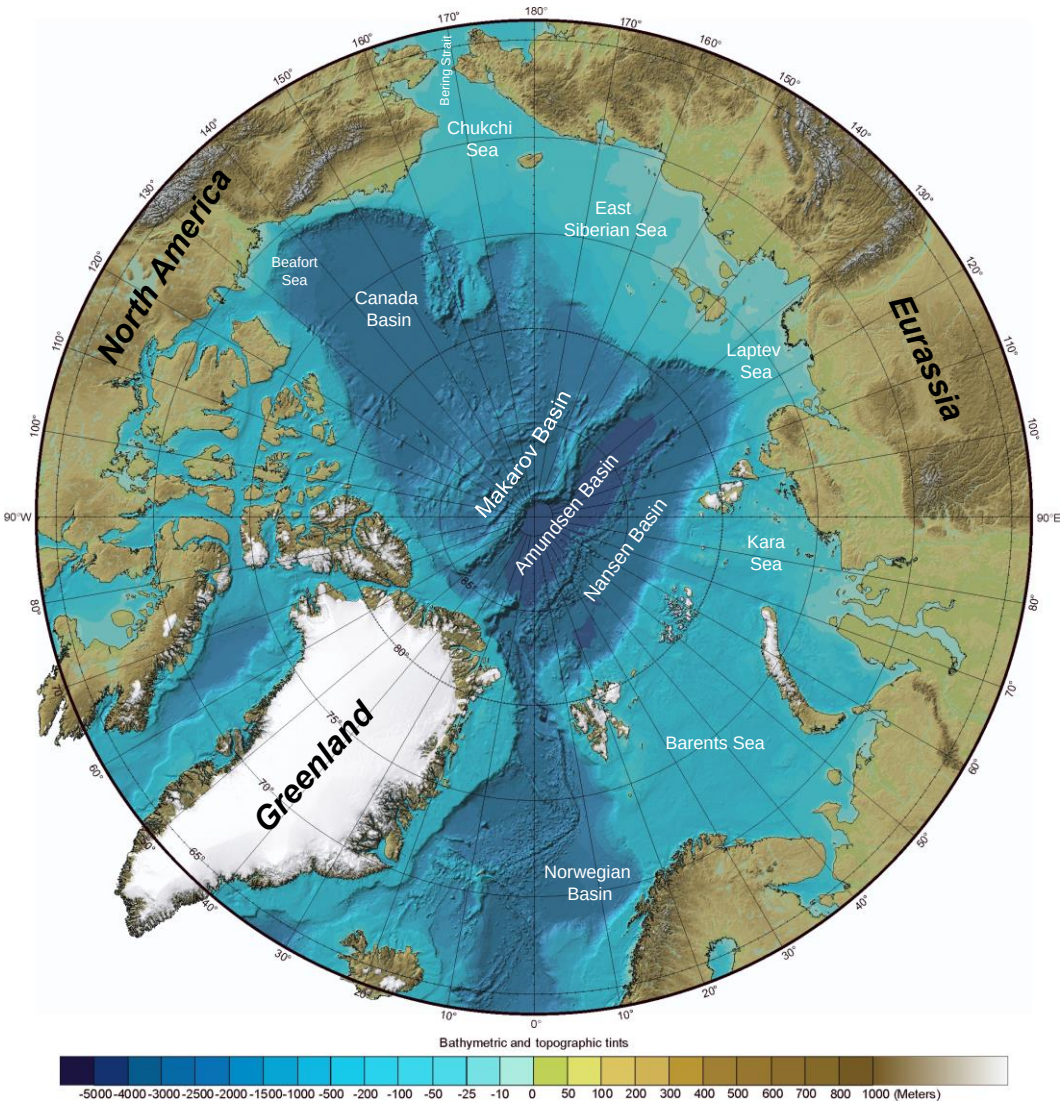

Fig. 1-3 Map and bathymetry of the Arctic Ocean. (Edited based on The International Bathymetric Chart of the Arctic Ocean (IBCAO), Jakobsson et al., 2012)

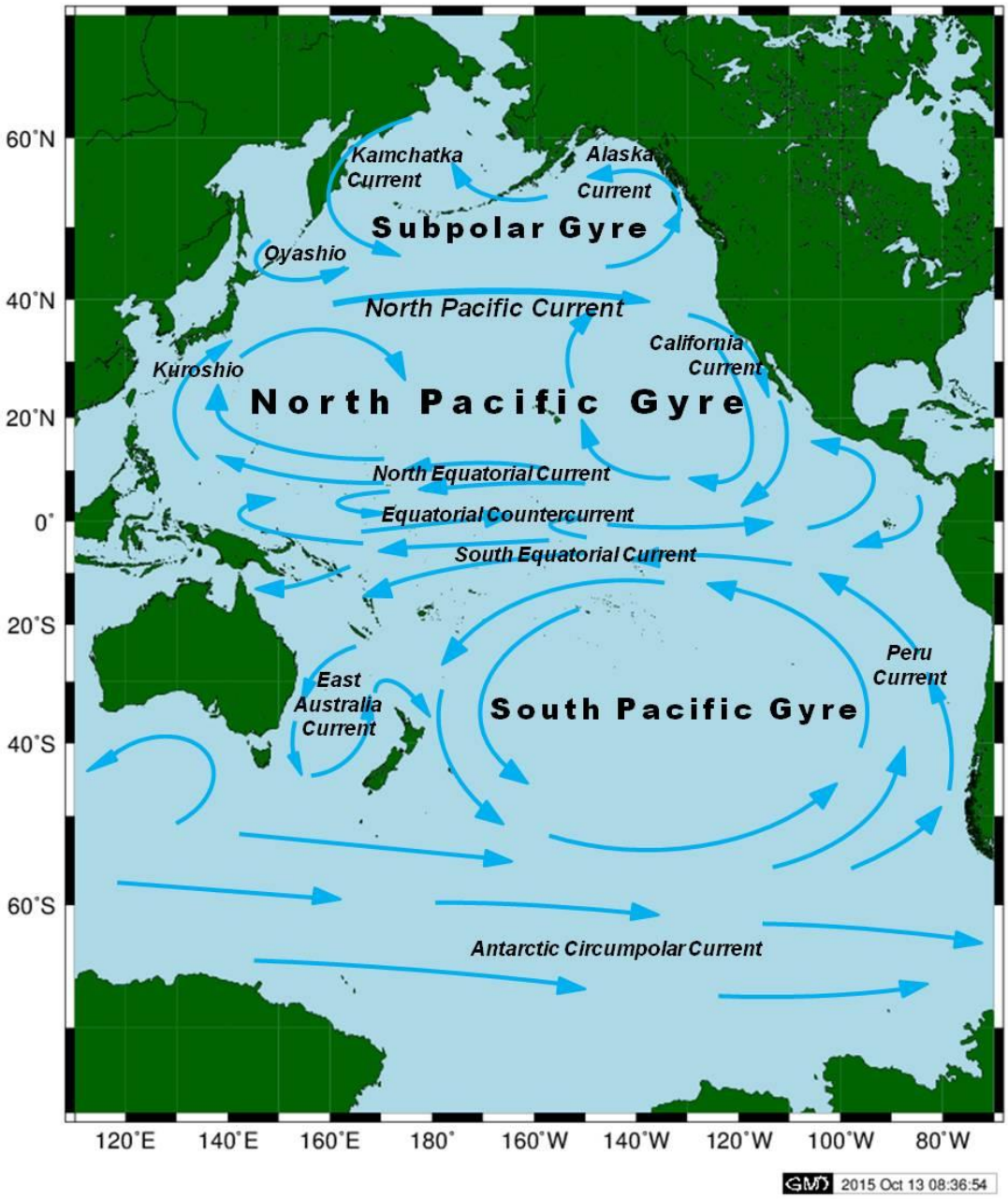

Fig. 1-4 Map and oceanography of the Pacific Ocean (Modified based on graph from http://www.seos-project.eu/modules/oceancurrents/oceancurrents-c02-p03.html)

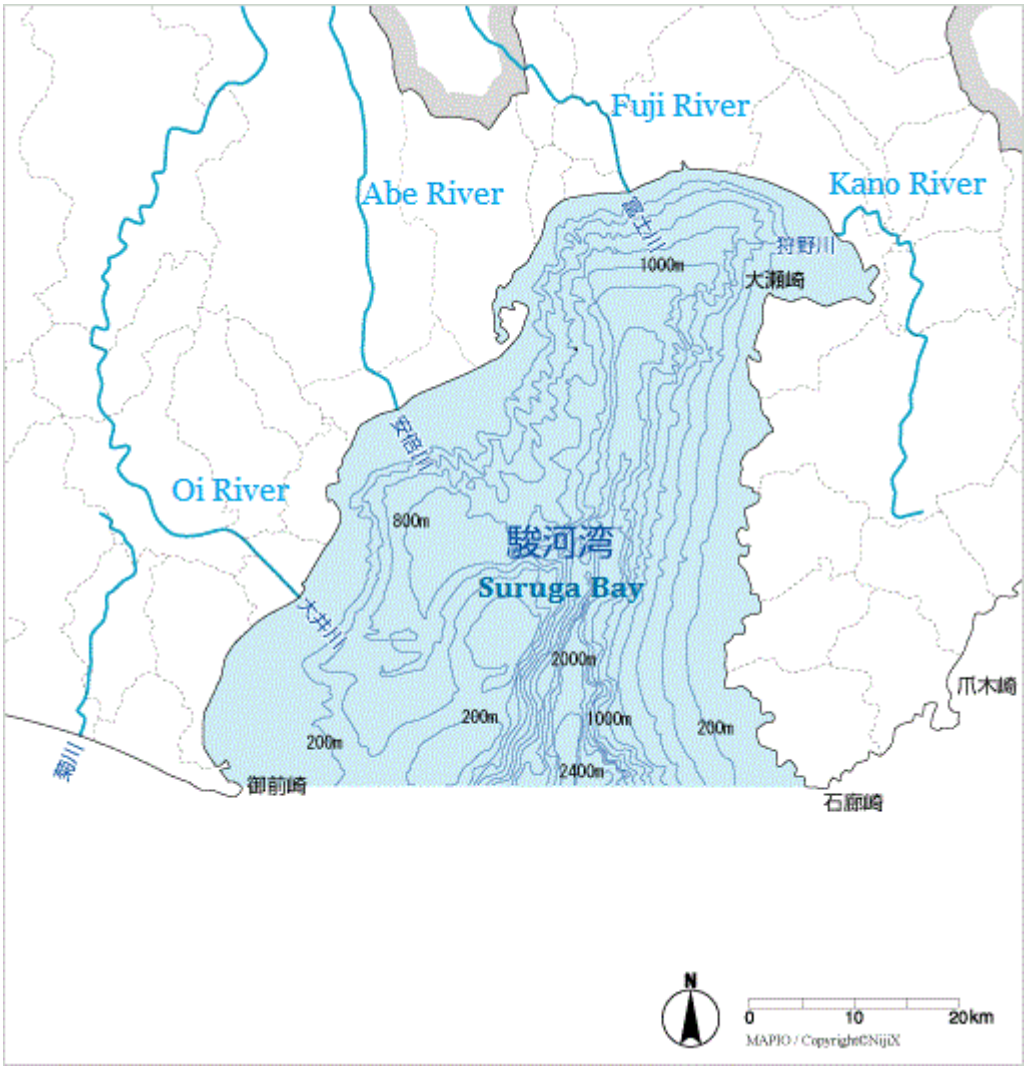

Fig. 1-5 Map and major rivers inflow of the Suruga Bay, Japan (Modified based on graph from http://www.isewan-db.go.jp/suruga-gaiyo/A2c.asp)

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